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INTRODUCTION

The small yellow tree frogs, *Hyla microcephala* and its relatives, are among the most frequently heard and commonly collected frogs in the lowlands of southern México and Central America. The similarities in size, proportions, and coloration of the different species have resulted not so much in a multiplicity of specific names, but in differences of opinion on the application of existing names to the various taxa. For example, the populations on the Atlantic lowlands have been known by three names, two of which have been applied to other taxa. Much of the confusion has been the result of previous workers' unfamiliarity with the animals in life and unawareness of the intraspecific geographic variation in the most widespread species.

Independently we undertook studies of these frogs in the field. The second author worked on the interspecific relationships and isolating mechanisms in Panamá (Fouquette, 1960b) and later studied the species in southern México. As part of his survey of the hylids of Middle America, the first author accumulated field and laboratory data on the frogs throughout their ranges in México and Central America. The purpose of this report is to present our findings on the four species of Middle American frogs that we place in the *Hyla microcephala* group. In addition to conventional taxonomic characters, we have utilized the features of the cranial osteology and have relied heavily on the data obtained from an analysis of the mating calls. Furthermore, we have included ecological and distributional data in our synthesis of interspecific relationships.

ACKNOWLEDGMENTS

Examination of specimens was made possible by the provision of working space at various institutions or through the loan of specimens. For their generosity in this manner we are grateful to Richard J. Baldauf, Charles M. Bogert, James E. Böhlke, Doris M. Cochran, Robert F. Inger, John M. Legler, Alan E. Leviton, Gerald Raun, Jay M. Savage, Hobart M. Smith, Robert C. Stebbins, Wilmer W. Tanner, Charles F. Walker, Ernest E. Williams, and Richard G. Zweifel.

Duellman is especially grateful to Charles W. Myers, Linda Trueb, Jerome B. Tulecke, and John Wellman for their assistance in the field and to Linda Trueb for her work on the cranial osteology that is incorporated in this report. Fouquette is indebted to H. Morgan Smith and A. C. Collins for assistance in the field, to A. J. Delahoussaye for assistance in the laboratory, and to W. Frank Blair for use of the facilities of the sound laboratory at the University of Texas and for much help in the early stages of this study.

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We are grateful to many persons, too numerous to mention, who in various ways aided our field work in Middle America. We are especially indebted to Dr. Rodolfo Hernandez Corzo and the late Ing. Luis Macías Arellano of the Dirección General de la Fauna Silvestre of the Mexican government for providing permits to collect in México.

Materials and Methods

For this report, data has been obtained from 2829 preserved frogs, 42 skeletal preparations, 8 lots of tadpoles and young, and 4 lots of eggs. Much of the material was collected in our independent field work, which has extended over a period of 11 years.

Measurements were taken in the manner described by Duellman (1956). Osteological data were obtained from specimens that were cleared in potassium hydroxide, stained with alizarin red, and stored in glycerine. Recordings were made by means of Magnemite portable tape recorders (Amplifier Corp. America). The calls recorded by Fouquette were analyzed on a Sonagraph (Kay Electric Co.) at the University of Texas; those recorded by Duellman were analyzed mainly on a Vibralyzer (Kay Electric Co.) at the University of Kansas and in part on a Sonagraph at the University of Southwestern Louisiana. Sample calls were analyzed on all three instruments; the slight differences in results were found to be less than the error in measurement, so the data from all sources were combined without correction. The techniques and terminology of the calls are those defined by Fouquette (1960a, 1960b).

In the accounts of the species we have attempted to give a complete synonymy. At the end of each species account the localities from which specimens were examined are listed alphabetically within each state, province, or department, which in turn are listed alphabetically within each country. The countries are arranged from north to south. Localities preceded by an

asterisk (*) are not plotted on the accompanying maps due to the crowding of symbols that would have resulted. Abbreviations for museum specimens are listed below:

AMNH—American Museum of Natural History
ANSP—Academy of Natural Sciences of Philadelphia
BMNH—British Museum (Natural History)
BYU—Brigham Young University
CAS—California Academy of Sciences
FMNH—Field Museum of Natural History
KU—University of Kansas Museum of Natural History
MCZ—Museum of Comparative Zoology
MVZ—Museum of Vertebrate Zoology
SU—Stanford University
UIMNH—University of Illinois Museum of Natural History
UMMZ—University of Michigan Museum of Zoology
USC—University of Southern California
USNM—United States National Museum
UU—University of Utah
TCWC—Texas Cooperative Wildlife Collection
TNHM—Texas Natural History Museum

HYLA MICROCEPHALA GROUP

Definition.—Small hylids attaining a maximum snout-vent length of 27 mm. in males and 32 mm. in females; dorsum yellowish tan with brown markings; thighs uniformly yellow, vocal sac in breeding males yellow; snout truncate in lateral profile; tympanum distinct, usually slightly smaller than one-half diameter of eye; vocal sac single, median, subgular; fingers about one-third webbed; toes webbed nearly to bases of discs, except only to middle of antepenultimate or base of penultimate phalanx of fourth toe; tarsal fold weak; inner metatarsal tubercle low, flat, elliptical; axillary membrane present; pupil horizontally elliptical; palpebral membrane unmarked; cranial elements reduced in ossification; sphenethmoid small, short; frontoparietal fontanelle large; tegmen tympani not extensive; quadratojugal greatly reduced; anterior arm of squamosal extending only about one-fourth distance to maxillary; posterior arm of squamosal not having bony connection with proötic; nasals lacking maxillary processes; medial ramus of pterygoid not having bony attachment to proötic; maxillary, premaxilary, and prevomerine teeth present; palatine and parasphenoid teeth absent; Mentomeckelians ossified; tadpoles having xiphicercal tails with deep caudal fins and terminal mouth lacking teeth; mating call consisting of one primary note followed by a series of shorter secondary notes; haploid number of chromosomes, 15 (known only in *H. microcephala* and *H. phlebodes*.)

Content.—As recognized here the *Hyla microcephala* group contains four species, one having two subspecies. An alphabetical list of the specific and subspecific names that we consider to be applicable to the *Hyla microcephala* group are listed below.

Names Proposed	Valid Names
Hyla cherrei Cope, 1894	? = *H. m. microcephala*
Hyla microcephala Cope, 1886	= *H. m. microcephala*
Hyla microcephala Boulenger, 1898 (*nec* Cope, 1886)	= *H. microcephala underwoodi*
Hyla microcephala martini Smith, 1951	= *H. microcephala underwoodi*
Hyla microcephala sartori Smith, 1951	= *H. sartori*
Hyla phlebodes Stejneger, 1906	= *H. phlebodes*
Hyla robertmertensi Taylor, 1937	= *H. robertmertensi*
Hyla underwoodi Boulenger, 1899	= *H. microcephala underwoodi*

Discussion.—The color pattern is the most useful character in distinguishing the species of the *Hyla microcephala* group from one another. Except in *Hyla microcephala,* little geographic variation in color pattern is noticeable. The features of color pattern that are helpful in identifying the species are: 1) presence or absence of lateral dark brown stripe; 2) longitudinal extent and width of lateral stripe, if present; 3) presence or absence of a narrow white line just dorsal to the lateral dark stripe; 4) presence or absence of an interorbital dark mark; 5) the arrangement of dark markings on the back, either as longitudinal lines or series of dashes, or in the form of various kinds of transverse markings; 6) presence of dark flecks, longitudinal line, or transverse marks on shanks.

Few consistent differences in measurements and proportions exist among the species (Table 1). The most obvious morphological difference is that the head is noticeably narrower in *H. robertmertensi* than in the other species. *Hyla phlebodes* is the smallest species; adult males attain snout-vent lengths of only 23.6 mm. The body is slender in *H. microcephala* and *robertmertensi,* slightly wider in *phlebodes,* and noticeably broader in *sartori.*

Distribution.—The composite range of the Middle American frogs of the *Hyla microcephala* group includes the lowlands of southern México and Central America, in some places to elevations of 1200 meters, southeastward from southern Jalisco and southern Veracruz, excluding arid regions (northern Yucatán Peninsula, Balsas-Tepalcatepec Basin, Plains of Tehuantepec, Grijalva Valley, Salamá Basin, and upper Motagua Valley) to the Pacific lowlands and the Cauca and Magdalena valleys in Colombia.

Key to Species and Subspecies

1. Lateral dark stripe, bordered above by narrow white line, extending from snout at least to sacral region 2
   Lateral dark stripe, if present, not extending posteriorly to sacral region and not bordered above by narrow white line 4
2. Lateral dark stripe continuous to groin; dark flecks or longitudinal line on shanks; interorbital dark bar absent; dorsal pattern usually consisting of pair of longitudinal dark lines or series of dashes 3
   Lateral dark stripe usually extending only to sacral region; dark transverse bars on shanks; interorbital bar usually present; dorsal pattern usually consisting of interconnecting dark lines, sometimes forming transverse marks ..... *H. microcephala underwoodi*
3. Lateral dark stripe narrow, covering only upper edge of tympanum; dorsal longitudinal stripes continuous, extending to vent *H. microcephala microcephala*
   Lateral dark stripe wide, encompassing entire tympanum; dorsal markings consisting of longitudinal series of flecks or dashes, or of two lines, usually not extending to vent ..... *H. robertmertensi*

4. Lateral dark stripe indistinct, present only above tympanum and insertion of arm; dorsal markings consisting of narrow lines and dashes, sometimes interconnected; transverse bars on shanks narrow relative to interspaces ..... *H. phlebodes*

Lateral dark stripe absent; dorsal markings consisting of two broad chevron-shaped marks; transverse bars on shanks wide relative to interspaces ..... *H. sartori*

ACCOUNTS OF SPECIES AND SUBSPECIES

Hyla microcephala Cope

Diagnosis.—Lateral dark stripe narrow, covering only upper edge of tympanum, bordered above by narrow white stripe; dorsal pattern consisting of pair of longitudinal brown lines and no interorbital bar (eastern populations), or of irregular dark markings forming an X- or) (-shaped mark in scapular region and an interorbital bar (western populations).

Content.—The populations inhabiting the Pacific lowlands of southeastern Costa Rica eastward to Colombia are recognized herein as *Hyla microcephala microcephala* Cope; the populations in western Costa Rica northward to México are assigned to *Hyla microcephala underwoodi* Boulenger.

Distribution.—Southern Veracruz and northern Oaxaca southeastward through the Atlantic lowlands of Central America to north-central Nicaragua, thence southeastward on the Pacific lowlands to eastern Panamá, and thence into the Cauca and Magdalena valleys (Caribbean drainage) of Colombia (Fig. 1).

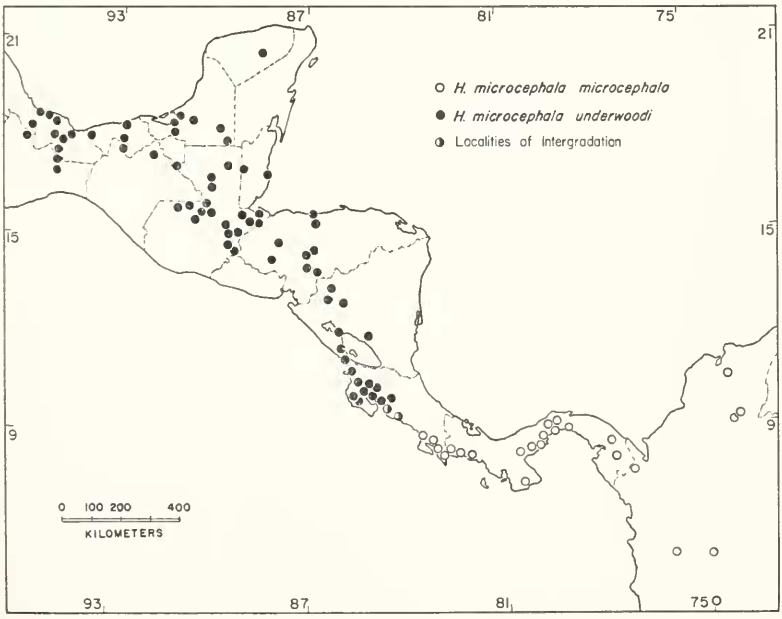


FIG. 1. Map showing locality records for *Hyla microcephala.*

TABLE 1.—Variation in Certain Measurements and Properties in the Hyla microcephala Group. (All Data Based on Adult Males; Mean and Standard Error of Mean Below Observed Range.)

LOCALITY	N	Snout-vent length (S-V L)	Tibia length / S-V L	Foot length / S-V L	Head length / S-V L	Head width / S-V L	Tympanum / Eye
				H. m. microcephala			
Panamá: Canal Zone.....	25	21.5–24.1 22.8±0.20	50.2–56.0 52.9±0.37	40.9–46.6 43.5±0.28	28.5–32.8 31.0±0.22	28.1–30.9 29.4±0.11	44.0–54.1 49.0±0.55
Costa Rica: Golfito.....	25	18.5–24.5 22.4±0.27	49.1–54.4 51.6±0.26	41.8–48.0 45.1±0.32	30.2–35.5 33.1±0.25	29.0–32.7 30.8±0.16	40.0–57.8 48.4±1.10
				H. m. underwoodi			
Nicaragua: La Cumplida...	25	23.0–25.6 21.1±0.19	51.0–55.7 52.9±0.25	41.3–46.5 43.7±0.25	29.7–33.5 31.6±0.19	28.9–31.8 30.4±0.17	42.3–60.0 49.3±0.97
Guatemala: Finca Chamá..	25	21.8–25.0 23.5±0.16	51.0–57.2 54.3±0.39	41.2–47.8 44.4±0.30	30.8–35.3 33.0±0.16	29.6–33.6 31.3±0.36	37.5–56.4 45.2±0.89
Tabasco: Teapa.....	25	22.7–25.8 24.3±0.14	48.0–54.5 51.5±0.29	40.7–46.8 43.3±0.25	29.5–33.0 31.7±0.17	28.7–31.8 30.3±0.16	40.7–53.8 45.5±0.38
Oaxaca: Donají-Sarabia....	25	22.1–25.9 23.8±0.19	49.8–55.6 52.8±0.33	40.5–46.6 43.4±0.27	30.4–34.8 32.8±0.19	28.9–32.6 30.8±0.17	37.0–54.1 45.1±0.76
Veracruz: Alvarado.....	25	21.9–25.4 21.1±0.17	49.6–54.4 51.1±0.28	40.7–47.5 42.6±0.34	29.9–33.8 31.4±0.18	29.1–32.9 30.5±0.17	40.7–53.8 46.6±0.65

LOCALITY	N	Snout-vent length (S-V L)	Tibia length / S-V L	Foot length / S-V L	Head length / S-V L	Head width / S-V L	Tympanum / Eye
				H. robertmertensi			
Guatemala: La Trinidad...	21	21.8–24.6 23.4±0.15	47.1–52.8 49.9±0.34	40.9–51.3 43.5±0.17	30.0–33.3 31.3±0.20	27.3–29.8 28.5±0.23	44.4–50.0 47.4±0.46
Chiapas: Acacoyagua.....	25	21.4–25.7 24.1±0.20	47.8–52.4 50.4±0.45	41.7–46.3 43.9±0.23	29.1–32.7 31.2±0.29	26.0–30.3 28.1±0.20	42.8–53.8 46.5±0.50
Oaxaca: Tapanatepec.....	25	22.4–26.4 24.7±0.18	44.1–48.3 46.4±0.23	39.1–44.5 41.7±0.23	26.1–30.4 28.4±0.16	25.4–28.1 26.8±0.14	45.8–58.3 52.9±0.77
				H. phlebodes			
Panamá: Canal Zone.....	25	19.6–23.2 22.2±0.16	49.1–56.9 52.8±0.35	41.9–47.1 45.4±0.26	33.6–37.4 34.8±0.18	32.3–36.0 33.8±0.18	37.9–46.4 41.6±0.49
Costa Rica: Turrialba.....	25	19.7–23.6 22.0±0.18	47.4–55.7 51.1±0.35	38.1–46.4 42.8±0.38	32.6–35.9 34.1±0.16	30.5–35.0 32.9±0.17	35.7–48.2 40.1±0.53
				H. sartori			
Guerrero: Tierra Colorada..	25	23.7–26.0 24.8±0.13	47.2–51.4 49.6±0.23	42.4–47.8 45.2±0.27	29.4–31.8 30.6±0.13	28.9–31.0 30.0±0.12	42.3–52.0 47.4±0.59

Hyla microcephala microcephala Cope

Hyla microcephala Cope, Proc. Amer. Philos. Soc., 23:281, February 11, 1886 [Syntypes.—USNM 13473 (2 specimens, now lost) from Chiriquí, Panamá; Mr. MacNeil collector]; Bull. U. S. Natl. Mus., 32:14, 1887. Günther, Biologia-Centrali Americana, Reptilia and Batrachia, p. 265, June, 1901. Dunn, Occas. Papers Boston Soc. Nat. Hist., 5:413, October 10, 1931; Occas. Papers Boston Soc. Nat. Hist., 8:72, June 7, 1933. Stebbins and Hendrickson, Univ. California Publ. Zool., 56:524, February 17, 1959. Fouquette, Evolution, 14:484, December 16, 1960. Busack, Copeia, 2:371, June 21, 1966.

? *Hyla cherrei* Cope, Proc. Acad. Nat. Sci. Philadelphia, 1894, p. 195, 1894 [Holotype.—location unknown, apparently lost; type-locality: "Alajuela, Costa Rica;" R. Alfaro collector]. Günther, Biologia Centrali-Americana: Reptilia and Batrachia, p. 264, June, 1901. Taylor, Univ. Kansas Sci. Bull., 35:846, July 1, 1952.

Hyla underwoodi, Ruthven, Misc. Publ. Mus. Zool., Univ. Michigan, 8:55, September 15, 1922. Barbour, Proc. New England Zool. Club, 10:31, March 2, 1928.

Hyla microcephala microcephala, Smith, Herpetologica, 7:185, December 31, 1951. Taylor, Univ. Kansas Sci. Bull., 39:23, November 18, 1958.

Diagnosis.—Brown lateral stripe narrow, extending from nostril along canthus, along upper edge of tympanum to groin, bordered above by narrow white line; pair of dark brown longitudinal lines on dorsum extending to vent; shanks having dark longitudinal line or flecks, no transverse bars; interorbital dark mark lacking.

Description and Variation.—The color pattern is nearly constant. Of 103 males from the Canal Zone, all lack an interorbital dark bar, and all have a dark longitudinal line on the dorsal surface of the shank and a narrow lateral dark stripe, bordered above by a narrow white line, extending to the groin. The longitudinal dark lines on the dorsum are continuous to the groin in 95 specimens and fragmented in two specimens. In two others the lines converge and fuse in the scapular region, and in four specimens auxiliary, fragmented lines are present dorsolaterally.

In all specimens from southeastern Costa Rica (Golfito, Palmar Sur, and Villa Neilly) the pattern is constant, except that in about 10 per cent of the specimens the longitudinal line on the dorsal surface of the shank is replaced by a row of brown flecks.

Of the limited number of Colombian specimens examined, all are patterned normally, except three from Sautata, Chocó, three from Curumani, and three from Arcataca, Magdalena, which have flecks on the dorsal surfaces of the shanks, and one from Espinal, Tolima, which has no markings on the shanks.

When active at night most individuals are pale yellowish tan dorsally; the white dorsolateral line is noticeable, but the brown lateral stripe, dorsal brown lines, and lines on shanks are so pale that often they are barely discernible. By day the dorsum changes to tan or pale reddish brown; the stripes are dark brown, and the dorsolateral stripe that is white at night becomes creamy yellow (Pl. 13). Small brown flecks are present on the dorsum of most individuals. The venter always is white, and the iris is pale bronze with a brown tint immediately anterior and posterior to the pupil. In breeding males the vocal sac is pale yellow.

Tadpoles.—Tadpoles of this species have been found in weed-choked ponds in eastern Panamá Province. The following description is based on KU 104097, a specimen in developmental stage 34 (Gosner, 1960).

Total length, 20.5 mm.; body length, 8.2 mm.; body slightly wider than deep; snout pointed; nostrils large, situated dorsally, much closer to snout than eyes, directed anteriorly; eyes moderately small, situated dorsolaterally and directed laterally; spiracle sinistral, located just posteroventral to eye; anal tube dextral. Tail xiphicercal; caudal musculature moderately deep, becoming slender posteriorly, extending beyond caudal fin; fins deepest at about one-third distance from body to tip of tail; dorsal fin extending onto body, deeper than deepest part of caudal musculature; ventral fin slightly shallower than musculature. Mouth small, terminal, lacking teeth and fringing papillae, but having finely serrate beaks. In preservative, top of head pale brown; dark stripe from tip of snout through eye to posterior edge of body, narrowing to thin line on proximal one-fourth of tail; venter white; tail creamy tan with fine black flecks most numerous posteriorly; posterior two-thirds of fins edged with black. In life, top of head yellowish tan; lateral stripe brown; belly white; anterior half of tail lacking pigment; posterior half deep orange; iris pale bronze (Pl. 15).

Remarks.—Evidence for intergradation of *Hyla microcephala* with *H. underwoodi* is provided by four specimens [USC 818 (2), 6081-2] from 6.1 kilometers northeast of the mouth of the Río Tarcoles, and nine specimens [USC 8254 (2), 8255, 8256 (4), 8258 (2)] from Parrita, both in Puntarenas Province, Costa Rica. These localities lie about two-thirds the distance from the northwesternmost locality for *H. m. microcephala* (Palmar Sur) to the southeasternmost locality for *H. m. underwoodi* (Barranca). Although in most aspects of coloration the frogs are more nearly like *H. m. underwoodi* than *H. m. microcephala*, some specimens have longitudinal lines on their shanks, such as are characteristic of *H. m. microcephala*. The dorsal pattern varies from nearly complete longitudinal lines to broken lines, fused into an X-shaped scapular mark or not.

As noted by Rivero (1961:135), *Hyla microcephala* seems to be closely related to *Hyla misera* Werner, a species having a wide distribution east of the Andes in South America. Despite the similarity in color pattern, size, and structure, we are reluctant to place the two taxa in the same species until data on coloration in life, mating calls, and life history are available for *Hyla misera* and compared with those of *Hyla microcephala*.

The status of Cope's *Hyla cherrei* is questionable. Since the type, the only specimen ever referred to the species, apparently is lost, the only extant information regarding the taxon is contained in the original description (Cope, 1894). There the species was characterized as having a narrow dorsolateral white stripe and lacking pigment on the upper arms and thighs. These characteristics of the color pattern combined with the statements "vomerine teeth few, opposite the middle of the very large choanae" and

"tympanic drum distinct, one half the area of eye" serve to distinguish *H. cherrei* from all other Costa Rican hylids, except *H. m. microcephala* and *H. m. underwoodi*. No statements in the type description will definitely associate *cherrei* with one or the other of these subspecies. Since it seems obvious that *H. cherrei* can be associated with *H. microcephala*, we prefer to place the name in the synonymy of the nominate subspecies, thereby preserving the commonly used name *H. underwoodi* (Boulenger, 1899) as a subspecies of *H. microcephala*.

Distribution.—*Hyla microcephala microcephala* inhabits coastal lowlands from the area of Golfo Dulce (apparently absent from the Osa Peninsula) in southeastern Costa Rica eastward in Panamá, including the Azuero Peninsula to northern Colombia and thence southward in the valleys of the Río Cauca and Río Magdalena in Colombia (Fig. 1). Except for the central area of the Canal Zone the subspecies is unknown from the Caribbean drainage in Central America, but in Colombia the subspecies occurs only in the Caribbean drainage. In Central America this frog occurs mostly on the coastal lowlands; the highest recorded elevation is 560 meters at El Valle, Coclé, Panamá. Throughout most of its range *Hyla microcephala microcephala* occurs in disturbed habitats —cut-over forests, secondary growth, and pastureland. It does not seem to be an inhabitant of either primary forest or of *Curatella*-savanna.

Specimens examined.—522, as follows: **Costa Rica:** Puntarenas: Golfito, KU 32172-207; 3 km. E Golfito, KU 86399, USC 2757-8; Palmar Sur, KU 64591-608, USC 2650 (14), UU 3907-32; °1.5-2.5 km. ESE Palmar Sur, KU 68293-7 (skeletons), 93957-62; Parrita, USC 8254 (2), 8255, 8256 (4), 8258 (2) [intergrades with *H. m. underwoodi*]; 3 km. NW Piedras Blancas, KU 103689; 6.1 km. NE mouth of Río Tárcoles, USC 818 (2), 6081-2 [intergrades with *H. m. underwoodi*]; Villa Neilly, USC 2651; °1-5 km. WNW Villa Neilly, USC 6182-4, 8003 (4), 8031 (3), 8032; °10.5 km. WNW Villa Neilly, KU 64609-27, 68398 (eggs).

Panama: Canal Zone: Albrook Air Base, TNHC 23389, 23497; Balboa, ANSP 19555-6; °Fort Clayton, UIMNH 42008-12; °2.8 km. SW Fort Kobbe, KU 96015-25; °Frijoles, MCZ 19208; °Bamboa, MCZ 21507; °8.3 km. N Gatún Locks, TNHC 23441; °Juan Diaz, MCZ 13747; °Juan Mina, AMNH 55436-7, ANSP 21811-2, UMMZ 126734, 126735 (6), UU 3900-6; °8-14 km. N Miraflores Locks, TNHC 23374-88, 23390-409, 23411-38, 23440, 23442-60, 23462-76; 23478-83, 23492, 23555-60, 23562-76; °Río Chagres, AMNH 55430, 55439; °Río Cocolí, 3.5 km. N Miraflores Locks, TNHC 23410; °Summit, ANSP 23365-71, FMNH 22966-9, KU 97783-87. Chiriquí: 5.5 km. E Concepción, AMNH 69772; °14.4 km. E Concepción, AMNH 69773-8; 2 km. S David, AMNH 69779; °Progreso, UMMZ 58252, 58253 (2), 58254, 58436; Río Gariché, 8.3 km. ESE Paso Canoas, KU 103065-8. Coclé: 1 km. SE El Caño, KU 103042-51; El Valle de Antón, AMNH 59614-18 (10), 69785, ANSP 23502-5, KU 77201-14, MVZ 66578-83, UIMNH 46532. Colón: Cement Plant, Transisthmian Highway, FMNH 60394-5. Darién: El Real, KU 80454-5, 103052-64, UMMZ 125036 (10), USNM 140567-8; Río Canclon at Río Chucunaque, UMMZ 125035; °Río Chucunaque, near Yavisa, AMNH 59523. Los Santos: Tonosí, KU 101606-9. Panamá: 5 km. S Bejuco, AMNH 69782; 3 km. W Chepo, KU 77172-4, 104097-8 (tadpoles); °6 km. WSW Chepo, KU 77175; °Chico, Río La Jagua, USNM 129070; °La Joya, Cacora, ANSP 25129-33; Madden Dam, FMNH 67819; Nueva Gorgona, AMNH 69780-1; °1.6 km. W Nueva Gorgona, AMNH 69783-4; 1.5 km. W Pacora, 77176-200; °Río La Laja, near Chamé, ANSP 21845; °Río Tapia, MCZ 10048; °Tapia, AMNH 18930, 18950, 18952-3; °18 km. E Tocumen, MVZ 78662.

Colombia: Chocó: Sautatá, Atrato, FMNH 74918 (2), 74919. Magdalena: Aracataca, ANSP 19755-7; Curumani, MCZ 21465-74, UIMNH 28855; UMMZ 90168, USNM 118247; El Banco, Río Magdalena, ANSP 25061; Fundación, UMMZ 48281-2. Tolima: Espinal, MCZ 15068; Mariquita, FMNH 81822-3. Valle: Sevilla, MCZ 13751-3.

Hyla microcephala underwoodi Boulenger

Hyla microcephala Boulenger, Proc. Zool. Soc. London, p. 481, October 1, 1898 [Syntypes.—BMNH 94. 11. 1532-33 from Bebedero, Guanacaste Province, Costa Rica; C. F. Underwood collector] (not *Hyla microcephala* Cope, Proc. Amer. Philos. Soc., 23:281, February 11, 1886, from Chiriquí, Panamá).

Hyla underwoodi Boulenger, Ann. Mag. Nat. Hist., ser. 7, 3:277, April, 1899 (substitute name for *Hyla microcephala* Boulenger, preoccupied). Günther, Biologia-Centrali Americana, Reptilia and Batrachia, p. 278, September, 1901. Dunn and Emlen, Proc. Acad. Nat. Sci. Philadelphia, 84:25, March 22, 1932. Stuart, Misc. Publ. Mus. Zool., Univ. Michigan, 29:39, October 1, 1935. Taylor, Proc. Biol. Soc. Washington, 50:44, April 21, 1937. Stuart, Occas. Papers Mus. Zool., Univ. Michigan, 471:15, May 17, 1943. Taylor and Smith, Proc. U. S. Natl. Mus., 95:586, June 30, 1945. Stuart, Misc. Publ. Mus. Zool., Univ. Michigan, 69:35, June 12, 1948. Smith and Taylor, Bull. U. S. Natl. Mus., 194:85, June 17, 1948; Univ. Kansas Sci. Bull., 33:316, March 20, 1950. Stuart, Contr. Lab. Vert. Biol., Univ. Michigan, 45:48, May, 1950. Taylor, Univ. Kansas Sci. Bull., 35:891, July 1, 1952; Univ. Kansas Sci. Bull., 39:25, November 18, 1958.

Hyla phlebodes, Cole and Barbour, Bull. Mus. Comp. Zool., 50:154, November, 1906. Kellogg, Bull. U. S. Natl. Mus., 160:172, March 31, 1932.

Hyla microcephala martini Smith, Herpetologica, 7:187, December 31, 1951 [Holotype.—UIMNH 20965 from Encarnacion, Campeche, México; H. M. Smith collector]. Stuart, Contr. Lab. Vert. Biol., Univ. Michigan, 68:46, November, 1954. Fugler and Webb, Herpetologica, 13:105, July 10, 1957. Stuart, Contr. Lab. Vert. Biol., Univ. Michigan, 75:17, June, 1958. Neill and Allen, Publ. Research Div., Ross Allen's Reptile Inst., 2:26, November 10, 1959. Duellman, Univ. Kansas Publ., Mus. Nat. Hist., 13:62, August 16, 1960. Stuart, Herpetologica, 17:74, July 11, 1961. Hensley and Smith, Herpetologica, 18:70, April 9, 1962. Stuart, Misc. Publ. Mus. Zool., Univ. Michigan, 122:36, April 2, 1963. Holman and Birkenholz, Herpetologica, 19:144, July 3, 1963. Duellman, Univ. Kansas Publ., Mus. Nat. Hist., 15:225, October 4, 1963; Univ. Kansas Publ., Mus. Nat. Hist., 15:588, June 22, 1965.

Hyla microcephala underwoodi, Smith, Herpetologica, 7:188, December 31, 1951.

Diagnosis.—Brown lateral stripe narrow, extending to groin or only to sacral region, bordered above by narrow white line; dorsal pattern bold, consisting of X- or)(-shaped mark in scapular region or pair of interconnected dark lines on back; interorbital dark mark usually present; shanks usually having dark transverse bars.

Description and Variation.—The dorsal color pattern is highly variable. The various permutations of the X-shaped scapular mark and dark sacral marks differ proportionately in different samples. The variation in color pattern in 12 samples is summarized in Table 2. In samples from the southern part of the range (southern Nicaragua and Guanacaste Province, Costa Rica) more (40-93%) individuals have the lateral stripes extending to the groin than in northern samples (0-42%) from southern México and Guatemala. Likewise, the percentage of specimens lacking bars on the shanks and a dark interorbital bar is higher in the Costa Rican samples than elsewhere in the range. The

Table 2.—Variation in Color Pattern in Hyla microcephala underwoodi

Population	N	Shanks		Inter-orbital bar		Dorso-lateral stripe		Scapular markings				Sacral markings		
		Bars	Flecks	Present	Absent	Groin	Sacrum	X	)(	||	Other	^	/\	Other
Oaxaca: Donají-Sarabia	27	22	5	27	0	0	27	23	4	0	0	7	6	14
Tabasco: Teapa-Villahermosa	55	46	9	55	0	0	55	53	2	0	0	19	11	23
Guatemala: La Libertad	51	51	0	51	0	17	34	45	6	0	0	16	14	21
Guatemala: Finca Chamá	32	32	0	32	0	0	32	32	0	0	0	26	2	4
Guatemala: Puerto Barrios	31	31	0	31	0	14	17	23	0	4	4	6	4	21
Honduras: Lago Yojoa	13	13	0	13	0	9	4	3	2	3	5	2	1	10
Nicaragua: La Cumplida	56	44	12	54	2	13	43	11	35	8	2	0	19	37
Nicaragua: Tipitapa	10	10	0	10	0	8	2	0	5	3	2	0	3	7
Nicaragua: Santo Thomás	10	10	0	10	0	8	2	3	0	7	0	0	5	5
Costa Rica: Tenorio-Tilarán	12	0	12	6	6	7	5	0	0	12	0	0	0	12
Costa Rica: Las Cañas-Liberia	38	21*	15	34	4	25	13	0	11	19	8	0	0	38
Costa Rica: Esparta	32	26	6	29	3	30	2	0	0	14	18	0	0	32

*Longitudinal stripes present in two specimens.

X- or)(-shaped scapular markings and /\- or / \-shaped sacral markings are most prevalent in northern samples, whereas to the south the dorsal markings are more commonly arranged in a pattern of paired lines, which usually are discontinuous and usually extend posteriorly only to the sacral region. Thus, the color pattern in *H. m. underwoodi* in the southern part of its range shows trends towards the pattern characteristic of *H. m. microcephala*. Intergrades between these two subspecies have been discussed in the account of the nominate subspecies.

When this frog is active at night its dorsum is pale yellow; faint flecks are present in some individuals. The white dorsolateral line usually is evident in the tympanic region, but in many individuals a dorsal pattern of lines and other marks is not evident. By day the dorsum changes to yellowish tan or pale brown with dark brown or reddish brown markings (Pl. 13). The venter is white, and the vocal sac in breeding males is yellow. The iris is pale bronze with a brown tint anterior and posterior to the pupil.

Remarks.—Hyla microcephala underwoodi has had a confused nomenclatural history. The taxon was first named *Hyla microcephala* by Boulenger (1898); this name was preoccupied by *Hyla microcephala* Cope (1886). Cole and Barbour (1906) and Kellogg (1932) used the name *Hyla phlebodes* Stejneger (1906) for specimens of this frog from México. Dunn (1931, 1933, 1934) applied the name *Hyla underwoodi* to Panamanian specimens that we identify as *Hyla phlebodes*. Smith (1951) named *Hyla microcephala martini* from southern México and Guatemala and considered the northern populations to represent a subspecies distinct from the Costa Rican *Hyla microcephala underwoodi*, despite the fact the Stuart (1935:39) stated that comparisons of specimens from El Petén, Guatemala, with the holotype of *Hyla underwoodi* showed only trivial differences.

Much of the confusion regarding the name *Hyla underwoodi* stems from the illustration given by Boulenger (1898:pl. 39, fig. 3) and reproduced by Taylor (1952:892), which shows a frog having a unicolor dorsum, dorsolateral white lines, and dark flanks. This pattern is in marked contrast to the pattern seen in most preserved specimens, which have the dorsum variously marked by dark brown lines or irregular marks. Smith (1951:185), in his description of *Hyla microcephala martini* from southern México, considered *H. underwoodi* to be a subspecies of *H. microcephala* that lacked dorsal dark markings.

Data accumulated in 1961 through field studies by the senior author at the type locality, Bebedero, and other localities in Guanacaste and Puntarenas provinces in Costa Rica provide a reasonable explanation of the differences in color pattern. As noted in the preceding description of this subspecies, at night the dorsal mark-

ings are not evident in many living individuals, whereas by day the dorsal markings are prominent. Most collectors prepare their specimens by day; consequently the majority of specimens have a pronounced dorsal pattern. Of the frogs collected in Costa Rica in 1961, some specimens were preserved at night; others from the same series were preserved by day. The differences are striking. In those preserved at night, dorsal markings are faint, if present at all. Some specimens closely match the figure given by Boulenger (1898).

It is extremely doubtful if the frog described and illustrated by Boulenger could be associated with either *Hyla phlebodes or H. microcephala microcephala*. Individuals of the former species lack a dorsolateral white line and always have some dorsal markings evident at night; furthermore, *H. phlebodes* is not known to occur on the Pacific lowlands. *Hyla microcephala microcephala* occurs farther southeast. Since there is no reason to doubt the type locality of *H. underwoodi*, since specimens from the area around the type locality that have been preserved at night are like the holotype in pattern, and since the characteristics of the populations of the frogs in Guanacaste are the same as, or gradually blend into those of, populations in northern Central America and southern México, the frogs from throughout the entire range can be referred to one taxon, the earliest name for which is *Hyla underwoodi* Boulenger, which herein is considered to be a subspecies of *H. microcephala* Cope.

Distribution.—Hyla microcephala underwoodi inhabits the Atlantic slopes and lowlands from southern Veracruz and extreme northern Oaxaca eastward across the base of the Yucatan Peninsula (possibly the species is extant in the northern part of the peninsula) to British Honduras and thence southeastward through the Caribbean lowlands and interior valleys in Honduras to central Nicaragua, where it apparently avoids the forested Caribbean lowlands and the dry Pacific lowlands of northwestern Nicaragua, but in the vicinity of Managua invades the Pacific lowlands and continues southward into northwestern Costa Rica as far as the Puntarenas Peninsula (Fig. 1). In México and Guatemala the species has not been taken at elevations of more than 350 meters, whereas farther south it occurs at higher elevations—780 meters at Silencio, Costa Rica, 830 meters on Montaña de Guaimaca, Honduras, 960 meters at Finca Tepeyac, Nicaragua, and 1200 meters at Finca Venecia, Nicaragua.

Specimens examined.—1270, as follows: **Mexico:** Campeche: Balchacaj, FMNH 100406, UIMNH 20944-6; Encarnación, FMNH 27069-70, 75784, MCZ 28360, 29637, UIMNH 20948-58, 20965, USNM 134264-5; Escárcega, UMMZ 122999; *7.5 km. W Escárcega, KU 71229-43; Laguna Alvarado, 65 km. S Xpujil, KU 75084-9; Pacaitún, Río Candelaria, FMNH 83118-20; *Tres Brazos, FMNH 113101-22, UIMNH 20947; 10 km. W Xpujil, KU 75082-3. Chiapas: Palenque, UIMNH 47984, 49139-50, USNM 114973-8. Oaxaca: *5 km. N Chiltepec, KU 87015-23; 3 km. N Donají UMMZ 115249 (9); *3.7 km. N Donají, UMMZ 115250 (5); *43 km. N Matías Romero, UIMNH 42550-68; *3.5 km. N Palomares, TNHC 25185, 25321-31, 25341-68; 4.6 km.

N Sarabia, UMMZ 115247 (2); °6.1 km. N Sarabia, UMMZ 115248 (11), °3 km. N Tolocita, KU 39655; Tuxtepec, KU 87024-40. Tabasco: 24 km. N Frontera, MCZ 35665-70; 0.8 km. E Río Tonolá, TNHC 25189; Teapa, UMMZ 119218 (4); °2.7 km. N Teapa, UMMZ 119216 (4); °10 km. N Teapa, UMMZ 119217 (6); °11.5 km. N Teapa, UMMZ 119219; °15.2 km. N Teapa, UMMZ 119220 (4); °17.6 km. N Teapa, UMMZ 119221 (12), 3.3 km. S Villahermosa, UMMZ 119215 (12), °17.6 km. S Villahermosa, UMMZ 119214 (12). Veracruz: 2.1 km. N Acayucan, UIMNH 42547-9; °6.4 km. NW Acayucan, UMMZ 115254 (14); 1.6 km. ESE Alvarado, UMMZ 115258 (39); °2.4 km. ESE Alvarado, UMMZ 115251 (2); °4.5 km. S Aquilera, UMZ 115252 (21); °8 km. SW Coatzacoalcos, UMMZ 119213 (10); 2.2 km. E Cosoleacaque, UMMZ 119222 (26); 10 km. SE Hueyapan, UMMZ 115255; 0.8 km. S Lerdo de Tejada, UMMZ 122778; °3.6 km. NE Minatitlán, TNHC 25150-2; 1.9 km. S Naranja, UMMZ 115253 (3); 4.5 km. NE Novillero, UMMZ 115256; San Andrés Tuxtla, FMNH 113124-8, UIMNH 20942-3. Yucatán: Chichén-Itzá, FMNH 36570, MCZ 2463 (2).

British Honduras: Cayo: 6.2 km. S El Cayo, MCZ 37885-92. Stann Creek: Stann Creek, FMNH 49068.

Guatemala: Alta Verapaz: 28.3 km. N Campur, KU 64578-90; Chinajá, KU 57425; Cubilquitz, UMMZ 90887, 90888 (4); Finca Chamá, UMMZ 90879 (13), 90880 (4), 90881, 90882 (28), 90883 (12), 90884 (46), 90885 (39), 90886 (20); °Finca Tinaja, BYU 16032; Panzós, UMMZ 90889 (2). Chiquimula: Chiquimula, UMMZ 98113; 2 km. N Esquipulas, UMMZ 106844. El Petén: La Libertad, KU 57447-97, 59907-11 (skeletons), MCZ 21461, UMMZ 75332 (13), 75333 (11), 75334 (14), 75335 (10); Piedras Negras, FMNH 113123, UIMNH 20966; °5 km. S Piedras Negras, USNM 114951-72; Tikal, UMMZ 117981 (2); Toocog, 15 km. SE La Libertad, KU 57426-46. El Quiché: Finca Tesoro, UMMZ 89165 (5). Huehuetenango: Finca San Rafael, 16 km. SE Barillas, FMNH 40917-9. Izabal: Puerto Barrios, FMNH 20004-7; 8 km. S Puerto Barrios, KU 57507-37, 59991 (eggs), 59992 (tadpoles); Quirigua, CAS 69657-701; 2.5 km. NE Río Blanco, KU 57539; San Felipe, FMNH 35065. Zacapa: 14 km. ENE Mayuelas, KU 57502-6; 8 km. ENE Río Hondo, KU 57498-501.

Honduras: Atlantidad: La Ceiba, UMMZ 91948 (2), USNM 117593-600; Lancetilla, MCZ 17981. Cortes: Lago Yojoa, AMNH 54917-9, 54957, 55134, KU 64563-77. El Paraiso: Valle de Jamastran, AMNH 54807-12. Francisco-Morazan: El Zamorano, AMNH 54873-81, KU 103223, UMMZ 123101; Montaña de Guaimaca, AMNH 54900-4 (8); Ranch San Diego, 19 km. SW Guaimaca, AMNH 53939. Itibucá: Vieja Itibucá, AMNH 54912-3.

Nicaragua: Chontales: 3 km. SW Santo Tomás, KU 64770-9, 68308 (skeleton). Esteli: Finca Venecia, 7 km. N, 16 km. E Condega, KU 85296; 2.4 km. N Estelí, MCZ 28933-7. Managua: 12-13 km. E Managua, KU 85297-301; °10 km. SW Tipitapa, UMMZ 119977 (10). Matagalpa: °Finca Tepeyac, 10.5 km. N, 9 km. E Matagalpa, KU 85302-3; Hacienda La Cumplida, KU 64780-96, 68309-11 (skeletons), UMMZ 116482 (8), 116483 (23), 116484 (3), 116485 (5), 119984 (3). Rivas: °Finca Amayo, 13 km. S, 14 km. E Rivas, KU 85304-7; 16 km. S Rivas, MCZ 29011-7; °20.5 km. SE Rivas, KU 85308-10; 5 km. SE San Pablo, KU 43111-4.

Costa Rica: Guanacaste: Arenal, USC 6254 (2); °3 km. W Bagaces, USC 7019 (10); °3 km. NE Boca del Barranca, USC 8017 (21), °Finca San Bosco, USC 6272 (6), 6276 (3); °Guayabo de Bagaces, USC 7022 (4), 7023 (3), 7025; 12 km. S La Cruz, USC 8091 (2); °Laguna Arenal, USC 6262; °27 km. N Las Cañas, USC 8171 (6); °16 km. E Las Cañas, KU 102252-8; 16 km. SSE Las Cañas, KU 65090-5; °20 km. SE Las Cañas, KU 102251; Liberia, KU 36827-39; °7.3 km. N Liberia, USC 8096 (4); °10 km. N Liberia, USC 8085 (9); °7.5 km. SE Liberia, KU 65102-8, 68621-2 (skeletons); °14.7 km. S Liberia, USC 8238 (3); °4 km. W Liberia, KU 36847-57; 2 km. S Nicoya, USC 8230; °3-10 km. ESE Playa del Coco, USC 8012 (16), 8137 (14); °21.6 km. ESE Playa del Coco, USC 8138 (13); °Peñas Blancas, KU 102247-50; °Río Bebedero, 5 km. S Bebedero, KU 65089; °Río Higuerón, USC 7168 (2); Santa Cruz, USC 8232 (2); °Silencio, USC 6248; °Tenorio, KU 32313; Tilarán,

KU 36858-60; °2 km. E Tilarán, KU 86403, °5 km. NE Tilarán, KU 36840-6 USC 6269. Puntarenas: Barranca, KU 32305-12, °5 km. WNW Barranca, UMMZ 119976 (2); °10 km. E Esparta, KU 86400-2; 1 km. WNW Esparta, KU 65101; °4 km. WNW Esparta, KU 65088; °10 km. WNW Esparta, KU 65063-87, 68616-20 (skeletons); °12 km. WNW Esparta, KU 65096-100, USC 8251; 21.8 km. W San Ramón, USC 8242 (15).

Hyla robertmertensi Taylor

Hyla robertmertensi Taylor, Proc. Biol. Soc. Washington, 50:43, April 21, 1937 [Holotype.—CNHM 100096 (formerly EHT-HMS 2270) from Tapachula, Chiapas, México; H. M. Smith and E. H. Taylor collectors]. Smith and Taylor, Bull. U. S. Natl. Mus., 194:84, June 17, 1948; Univ. Kansas Sci. Bull., 33:326, March 20, 1950. Mertens. Senckenbergiana, 33:170, June 15, 1952; Senckenbergischen Naturf. Gesell., 487:30, December 1, 1952. Stuart, Contr. Lab. Vert. Biol., Univ. Michigan, 68:47, November, 1954. Duellman, Univ. Kansas Publ., Mus. Nat. Hist., 13:63, August 16, 1960. Duellman and Hoyt, Copeia, 1961 (2): 417, December 19, 1961. Porter, Herpetologica, 18:168, October 17, 1962. Stuart, Misc. Publ. Mus. Zool., Univ. Michigan, 122:36, April 2, 1963. Duellman and Trueb, Univ. Kansas Publ., Mus. Nat. Hist., 17:348, July 14, 1966.

Diganosis.—Brown lateral stripe wide, including loreal region and entire tympanum, extending to groin, bordered above by narrow white line; dorsum unicolor or with pair of dark lines (or rows of dashes) usually extending only to the sacral region; shanks having dark flecks, no transverse bars; interorbital bar lacking.

Description and Variation.—Males attain a maximum snout-vent length of 26.4 mm. in Oaxaca, whereas in a sample from Acacoyagua, Chiapas, the largest male has a snout-vent length of 25.7 mm., and from La Trinidad, Guatemala, 24-6 mm. Specimens from the western part of the range (eastern Oaxaca) have slightly smaller heads and proportionately larger tympani than the more eastern populations (Table 1).

The color pattern shows little variation, except in the nature of the dorsal markings. In a few specimens from throughout the range, but especially in the eastern part of the range, the dorsum lacks markings between the dorsolateral white lines. In most specimens the dorsal pattern consists of flecks or dashes arranged in two parallel longitudinal rows, and in some specimens the marks are fused into parallel lines. Small brown flecks are present on the dorsal surfaces of the shanks; in some specimens these flecks tend to form a longitudinal stripe on the shank. An interorbital dark mark is invariably absent.

When active at night *Hyla robertmertensi* is pale yellow above with a white dorsolateral line and pale brown lateral stripe; the dorsal markings are faint. By day the dorsum is yellowish tan with brown markings. The dorsolateral stripe is creamy white, and the lateral stripe is dark brown (Pl. 14). The venter is white, and the iris is dull bronze. In breeding males the vocal sac is yellow.

Remarks.—Although this species superficially resembles *Hyla microcephala microcephala,* the latter is easily distinguished by the narrow brown lateral stripe, as compared with the much wider stripe in *H. robertmertensi.* No other hylids in northern Central America and southern México can be confused with this species.

Distribution.—*Hyla robertmertensi* inhabits the Pacific slopes (to elevations of 700 meters) and lowlands from eastern Oaxaca (east of the Plains of Tehuan-

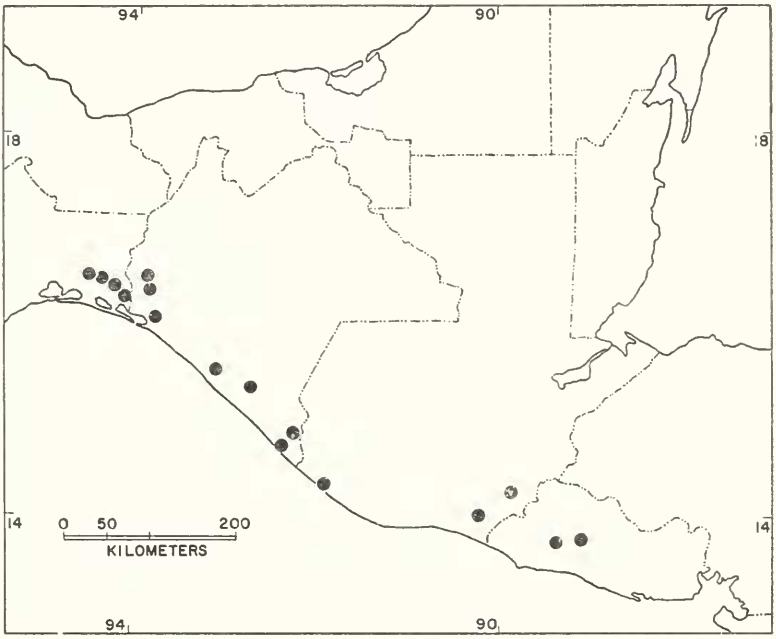


FIG. 2. Map showing locality records for *Hyla robertmertensi.*

tepec) southeastward to central El Salvador. The species also occurs in the Cintalapa Valley (Atlantic drainage) in southwestern Chiapas (Fig. 2.) The distribution seems to be limited on the northwest and southeast by arid environments. The region in which *Hyla robertmertensi* lives is characterized by higher rainfall and more luxuriant vegetation than occur on the Plains of Tehuantepec or on the Pacific lowlands of eastern El Salvador and southern Honduras. In addition to the localities listed below, Mertens (1952:30) recorded the species from Hacienda Cuyan-Cuya, Depto. Sonsonate, El Salvador.

Specimens examined.—490, as follows: **Mexico:** CHIAPAS: Acacoyagua, USNM 114754-61; °2 km. W Acacoyagua, UMMZ 87843 (28), 87844 (50), 87845 (50), 87846 (45), 87847 (27), 87848 (3); 32 km. N Arriaga, KU 57619-24, 59917-8 (skeletons); Asunción, FMNH 100413, 100501-4, UIMNH 26989-90, USNM 134267; °La Esperanza, USNM 114737-48, 114750-3, 17 km. S Las Cruces, KU 57625-49, 59997 (eggs); 8.5 km. N Puerto Madero, UMMZ 119981 (2); °11.7 km. N Puerto Madero, UMMZ 119982; Tapachula, FMNH 100096, UIMNH 26987; °11 km. S Tapachula, KU 57605-18, 59916 (skeleton); Tonolá, FMNH 27073, 100505-10, UIMNH 26988. OAXACA: Tapanatepec, UMMZ 115245 (2), °1.6 km. E Tapanatepec, UMMZ 115244 (14); °4.3 km. E Tapanatepec, UIMNH 38368-9; °7.5 km. W Tapanatepec, UMMZ 115246 (39); 12.8 km. W Tapanatepec, KU 65007-14; 7.2 km. WNW Zanatepec, UMMZ 115243 (77); °13.6 km. WNW Zanatepec, TNHC 25213-22; 22.7 km. WNW Zanatepec, TNHC 25203-9.

Guatemala: JUTIAPA: Jutiapa, UMMZ 106848; La Trinidad, UMMZ 107733 (23). RETALHUELEU: Casa Blanca, UMMZ 107732.

El Salvador: LA LIBERTAD: 16 km. NW Santa Tecla, KU 44112. SAN SALVADOR: 21.9 km. N San Salvador, UMMZ 119983 (6).

Hyla phlebodes Stejneger

Hyla phlebodes Stejneger, Proc. U. S. Natl. Mus., 30:817, June 4, 1906 [Holotype.—USNM 2997 from "San Carlos," Costa Rica; Burgdorf and Schild collectors]. Taylor, Proc. Biol. Soc. Washington, 50:44, April 21, 1937; Univ. Kansas Sci. Bull., 35:888, July 1, 1952; Univ. Kansas Sci. Bull., 39:25, November 18, 1958. Fouquette, Evolution, 14:484, December 16, 1960. Duellman and Trueb, Univ. Kansas Publ., Mus. Nat. Hist., 17:348, July 14, 1966.

Hyla underwoodi, Dunn, Occas. Papers Boston Soc. Nat. Hist., 5:413, October 10, 1931; Occas. Papers Boston Soc. Nat. Hist. 8:72, June 7, 1933; Amer. Mus. Novitiates, 747.2, September 17, 1934, Gaige, Hartweg, and Stuart, Occas. Papers Mus. Zool., Univ. Michigan, 357:5, October 26, 1937. Breder, 1946, Bull. Amer. Mus. Nat. Hist., 86:416, August 22, 1946.

Diagnosis.—Dark brown lateral stripe, if present, usually extending only to insertion of forearm, never posteriorly to sacral region; white line above brown stripe absent or faint; dorsal pattern weak, usually consisting of irregular dashes or interconnected lines; interorbital dark mark present; shanks having weakly defined transverse bars.

Description and variation.—In the majority of specimens (70%) the lateral dark stripe extends from the nostril to the eye and thence above the tympanum to a point above the insertion of the arm; in 17 per cent the stripe extends to the mid-flank, whereas in 13 per cent the stripe is absent. A narrow and faint white line is present on the canthus in some specimens, but no distinct white stripe is present above the lateral dark line posterior to the eye. An interorbital bar and transverse marks on the shanks are invariably present. The dorsal markings are variable, but in most specimens (92%) consist of either an X- or)(-shaped mark in the scapular region; in the other specimens the markings are irregular short lines or absent. Approximately equal numbers of specimens have a transverse bar, chevron, or broken lines in the sacral region, whereas about eight per cent of the specimens lack markings in the sacral region.

When active at night, individuals are pale yellowish tan with faint brown dorsal markings. By day they are tan with more distinct brown markings (Pl. 14). The thighs are pale yellow; the belly is white. The iris is pale creamy tan with brown flecks. In breeding males the vocal sac is yellow.

Tadpoles.—Tadpoles of this species have been found in an extensive grassy pond at Puerto Viejo, Costa Rica. The following description is based on KU 104099, a specimen in development stage 36 (Gosner, 1960).

Total length, 21.0 mm.; body length, 6.7 mm.; body slightly wider than deep, snout pointed; nostrils large, directed anteriorly, situated near end of snout; eyes small, situated dorsolaterally, directed laterally; spiracle sinistral, located just posteroventral to eye; anal tube dextral. Tail xiphicercal; caudal musculature moderately deep, extending far beyond posterior edge of fins; fins deepest at about midlength; dorsal fin extending onto body, slightly deeper than caudal musculature; ventral fin slightly shallower than musculature. Mouth small, terminal, lacking teeth and fringing papillae, but having finely serrate beaks. In preservative top of head olive-tan with brown flecks; dark stripe from snout through eye to posterior edge of body; belly white, flecked with brown anteriorly; tail creamy tan with grayish brown blotches. In life, dorsum of body reddish tan mottled with darker brown; lateral stripe dark brown; belly white, mottled with brown and black; caudal musculature heavily pigmented

with grayish tan; posterior tip of tail marked with dark gray; caudal fins heavily blotched with grayish tan; iris orange-tan peripherally, red centrally (Pl. 15).

Remarks.—This species has been confused with *Hyla microcephala underwoodi* by many workers. Dunn (1931, 1933, 1934) and Breder (1946) referred Panamanian specimens of *H. phlebodes* to *H. underwoodi;* likewise, Gaige, Hartweg, and Stuart (1937) made the same error. Cole and Barbour (1906) and Kellog (1932) used the name *H. phlebodes* for Mexican specimens of *H. microcephala underwoodi.* The similarity in color pattern of *H. microcephala underwoodi* and *H. phlebodes* easily accounts for the misapplication of names. Although both species have nearly identical dorsal color patterns, that of *H. microcephala underwoodi* usually is bolder. Furthermore, in that species a narrow white line usually is present above the well-defined lateral dark stripe, whereas the lateral dark stripe is short and posterior to the eye is not bordered above by a white line in *H. phlebodes.*

The type locality "San Carlos, Costa Rica" given by Stejneger (1906:817) apparently refers to a region, the Llanuras de San Carlos, in the northern part of Alajuela Province, Costa Rica.

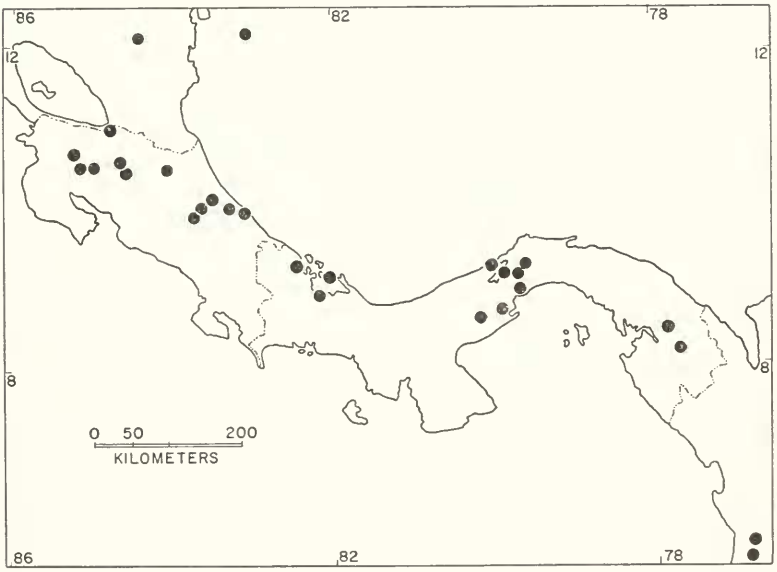


FIG. 3. Map showing locality records for *Hyla phlebodes.*

Distribution.—Hyla phlebodes inhabits humid tropical forests from southeastern Nicaragua southeastward on the Caribbean slopes and lowlands to the Canal Zone in Panamá, thence eastward in the Chucunaque Basin of eastern Panamá and onto the Pacific lowlands of Colombia (Fig. 3). The species also

reaches the Pacific slopes in the Arenal Depression in northwestern Costa Rica and in the Panamanian isthmus, where it occurs in humid forests on the Pacific slope of El Valle and Cerro La Campana. Mostly the species is found at low elevations, but it occurs at 600 meters at Turrialba and at 700 meters at Finca San Bosco in Costa Rica.

Specimens examined.—410, as follows: Nicaragua: Zelaya: Isla Grande del Maíz, MCZ 14848; Río Mico, El Recrero, UMMZ 79720 (6).

Costa Rica: Alajuela: 12.4 km. N Florencia, MVZ 76108-10, USC 2628; *Las Playuelas, 11 km. S Los Chiles, USC 7216; Los Chiles, USC 7217, 7219; 3 km. NE Muelle de Arenal, USC 2644 (2); *"San Carlos," USNM 29970. Cartago: Chitaría, KU 103690; *1.6 km. E Río Reventazón Bridge, east of Turrialba, UMMZ 119978 (2); *Tunnel Camp, near Peralta, KU 32456, 32458-69, 41098 (skeleton); Turrialba, FMNH 101794, 103188-9, KU 25725-9, 32439-48, 41095-7 (skeletons), 64797-827, 68300-2 (skeletons), 68403 (eggs), 68404 (tadpoles), MCZ 29224-5, 29310-2, UMMZ 119979 (6), USC 31, 256 (2), 458 (2), 580, 594, 599 (7), 7074 (2), USNM 29933. Guanacaste: Arenal, USC 6254; *Finca San Bosco, USC 62724), 6276 (3), Guayabo de Bagaces, USC 7022 (3), 7023; *Laguna Arenal, USC 6262 (4); 3 km. NE Tilarán, USC 524; *5 km. NE Tilarán, USC 6269; *6 km. NE Tilarán, UMMZ 122653 (6), S-2680 (skeleton), USC 523 (8). Heredia: Puerto Viejo, KU 64828-63, 68303-7 (skeletons), 68405-6 (tadpoles), 104099-100 (tadpoles); *1.5 km. N Puerto Viejo, KU 64871; *1 km. S Puerto Viejo, KU 86432-40; *4.2 km. W Puerto Viejo, KU 64864-5; *5.9 km. W Puerto Viejo, KU 64866-70; *7.5 km. W Puerto Viejo, KU 86431. Limón: Batán, UMMZ 119980 (2); La Castilla, ANSP 23707; Puerto Limón, KU 32449-55.

Panama: Bocas del Toro: 3.2 km. NW Almirante, KU 96026; Cayo de Agua, KU 96027-31; Fish Creek, KU 96032-4. Canal Zone: Barro Colorado Island, AMNH 69790, ANSP 23244-50; FMNH 13380, 22972-4; Juan Mina, AMNH 55429, UU 3899; *8.6-13.8 km. N Miraflores Locks, TNHC 23439, 23477, 23484-8, 23491, 23494-9, 23501-2, 23504-8, 23510-17, 23519-30, 23532-8, 23541-54, 23561. *Río Chagres, AMNH 55431-4; Río Cocolí, 3.5 km. N Miraflores Locks, TNHC 23461, 23489-90, 23493, 23500, 23503, 23509, 23518, 23531, 23539-40; *Summit, ANSP 23361, KU 97788; *Three Rivers Plantation, SU 2130. Coclé: El Valle de Antón, AMNH 55435, 69786-9, ANSP 23506-9. Colón: Achiote, KU 77215-78; Ciricito, CAS 71499-500, 71505-6. Darién: Río Canclon at Río Chucunaque, UMMZ 126733; Río Chucunaque, near Yavisa, AMNH 51783. Panamá: Cero La Campana, FMNH 67847-50.

Colombia: Chocó: Andagoya, FMNH 81856; Boca de Raspadura, AMNH 13570-8.

Hyla sartori Smith

Hyla underwoodi (in part), Smith and Taylor, Bull. U. S. Natl. Mus., 194:85, June 17, 1948.

Hyla microcephala sartori Smith, Herpetologica, 7:186, December 31, 1951 [Holotype.—UIMNH 20934 from 1 mile north of Organos, south of El Treinte, Guerrero, México; H. M. Smith and E. H. Taylor collectors]. Duellman, Univ. Kansas Publ., Mus. Nat. Hist., 15:124, December 20, 1961. Porter, Herpetologica, 18:168, October 17, 1962. Davis and Dixon, Herpetologica, 20:230, January 25, 1965. Duellman, Univ. Kansas Publ. Mus. Nat. Hist., 15:652, December 30, 1965.

Diagnosis.—Dorsum tan with broad dark brown chevrons or transverse bars; shanks marked with two or three broad transverse bars; dorsolateral stripes absent.

Description and variation.—No noticeable geographic variation is apparent in either structural features or coloration in this species. All specimens lack a dorsolateral dark stripe and white line, although a dark line is present on the

canthus and dissipates in the loreal region. A broad interorbital brown bar is present in all specimens. The color pattern on the dorsum invariably consists of a broad, dark, chevron-shaped mark in the scapular region and a broad dark chevron or transverse bar in the sacral region. The shanks invariably have two or three dark brown transverse bars.

When active at night individuals are yellowish tan above with chocolate brown markings (Pl. 14). The belly is white, and the thighs are pale yellowish tan. The iris is dark bronze-color. In breeding males the vocal sac is yellow. By day some individuals were observed to change to creamy gray with distinct darker markings.

Remarks.—Although tadpoles of this species have not been found, observations on the breeding sites indicate that the tadpoles probably develop in ponds. Except for calling males observed around a pool in a stream-bed 11.8 kilometers west-northwest of Tierra Colorada, Guerrero, all breeding congregations have been found at temporary ponds.

Smith (1951:186) named *Hyla sartori* as a subspecies *of Hyla microcephala.* This subspecific relationship seemed reasonable until analysis of the mating calls showed that the call of *H. sartori* is more nearly like that of *H. phlebodes* than that of *H. microcephala.* The broad hiatus separating the ranges of *H. microcephala* and *H. sartori* is additional evidence for considering *H. sartori* as a distinct species.

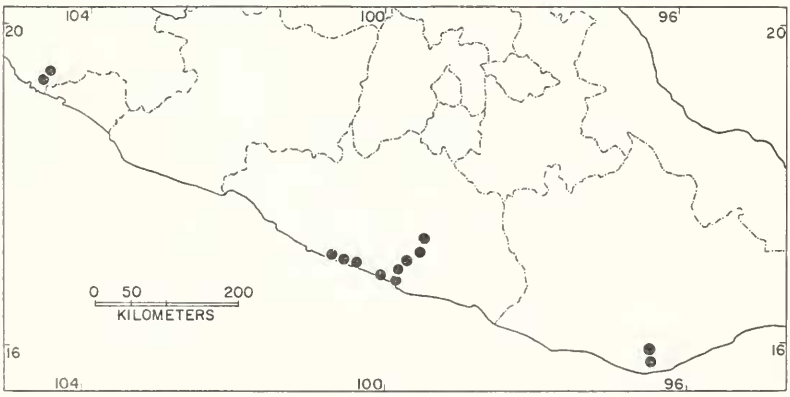


FIG. 4. Map showing locality records for *Hyla sartori.*

Distribution.—*Hyla sartori* occurs in mesophytic forests to elevations of about 300 meters on the Pacific slopes of southern México from southwestern Jalisco to south-central Oaxaca (Fig. 4). The lack of specimens from Colima and Michoacán probably reflects inadequate collecting instead of the absence of the species there. On the basis of available habitat the species would be expected to occur in Nayarit, but extensive collecting there has failed to reveal its presence. The semi-arid Plains of Tehuantepec apparently limit the distribution to the east.

Specimens examined.—190, as follows: México: Guerrero: 5 km. E Acapulco, AMNH 54611-2; 23.2 km. N Acapulco, UIMNH 26404-7; Colonia Buenas Aires, 23 km. E Tecpán de Galeana, UMMZ 119223 (7); *El Limoncito, FMNH 75785, 100390-402, 104631, 104633, UMMZ 117250, USNM 134266; El Treinte, FMNH 100403, UIMNH 20935-7; Laguna Coyuca, AMNH 59686; La Venta, MCZ 29635; * Morjonares, UIMNH 26392-402; 1.6 km. N Organos, FMNH 100404-5, UIMNH 20933-4; 19.2 km. S Petaquillas, UIMNH 26408; 6.1 km. E. Tecpán de Galeana, TNHC 23396-408; * 11.2 km. N Tierra Colorada, UIMNH 26403; 11.8 km. WNW Tierra Colorada, UMMZ 119225 (51), S-2677-9 (skeletons); Zacualpán, UMMZ 119224 (6). Jalisco: 6.4 km. NE La Resolana, KU 67853-69; 24 km NE La Resolana, KU 67870-3. Oaxaca: 3 km. N Pochutla, KU 57539; 13.4 km. N Pochutla, UMMZ 123495 (40).

CRANIAL OSTEOLOGY

The frogs of the *Hyla microcephala* group have a minimal amount of cranial ossification as compared to more generalized hylid skulls, such as *Smilisca* (Duellman and Trueb, 1966). In the *Hyla microcephala* group the sphenethmoid is small and short, and a large frontoparietal fontanelle is present. The quadratojugal exists only as a small spur and is not in contact with the maxillary. The proötics are poorly developed. The anterior and posterior arms of the squamosal are short; the anterior arm extends no more than one-fourth of the distance to the maxillary, and the posterior arm does not have a bony connection with the proötic. The nasal lacks a maxillary process, and the medial ramus of the pterygoid lacks a bony connection to the proötic.

Teeth are absent on the parasphenoid and palatines, but present on the maxillaries, premaxillaries, and prevomers. The teeth are simple, pointed, and slightly curved. Although the number of teeth varies (Table 3), no consistent differences between the species are apparent.

Table 3.—Variation in the Number of Teeth in the Species of the Hyla Microcephala Group. (N=Number of Jaws, or Twice the Number of Individuals; Means are Given in Parentheses After the Observed Ranges).

Species	N	Maxillary	Premaxillary	Prevomer
H. microcephala	32	31–47 (37.8)	4–13 (8.9)	2–4 (3.2)
H. phlebodes	10	38–45 (40.1)	8–13 (10.3)	2–5 (3.9)
H. robertmertensi	6	23–43 (32.8)	7–12 (10.5)	2–3 (2.7)
H. sartori	6	27–43 (38.2)	9–10 (9.3)	3–4 (3.7)

Despite the great reduction in the ossification of the cranial elements, certain apparently consistent differences exist between

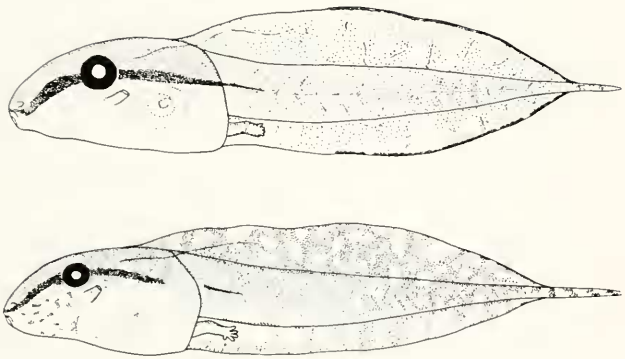
PLATE 13

Upper figure, *Hyla microcephala microcephala* (KU 64593); middle figure, *H. microcephala underwoodi* (KU 64565); lower figure, *H. microcephala underwoodi* (UMMZ 115247). All approximately $\times 3$.

PLATE 14

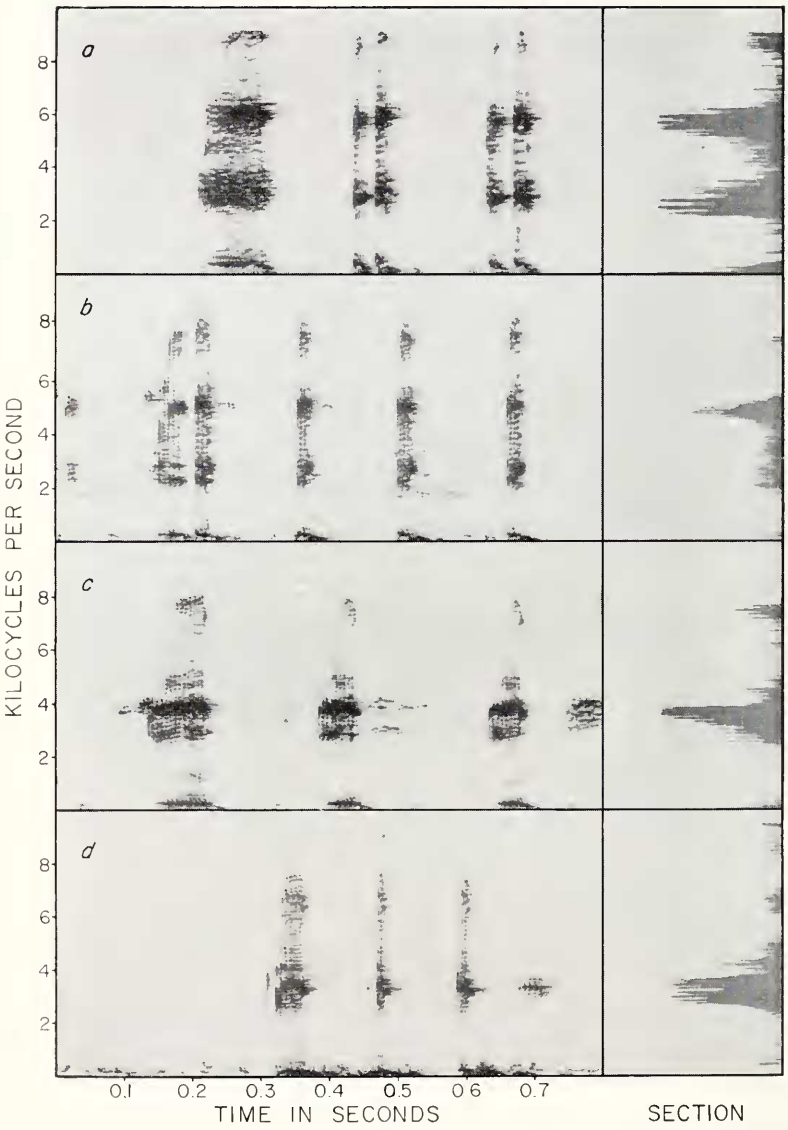
Upper figure, *Hyla robertmertensi* (UMMZ 115243); middle figure, *H. phlebodes* (KU 64798); lower figure, *H. sartori* (UMMZ 119225). All approximately × 3.

PLATE 15



Tadpoles of *Hyla microcephala* group: upper figure, *H. m. microcephala* (KU 104097); lower figure, *H. phlebodes* (KU 104099). Both × 4.

PLATE 16



Audiospectrograms and sections of mating calls of *Hyla microcephala* group: (a) *H. m. microcephala* (KU Tape No. 19); (b) *H. robertmertensi* (KU Tape No. 41); (c) *H. phlebodes* (KU Tape No. 6); (d) *H. sartori* (KU Tape No. 190).

TABLE 4.—Comparative Cranial Osteology of Hyla microcephala Group

CHARACTER	*H. microcephala*	*H. robertmertensi*	*H. phlebodes*	*H. sartori*
Frontoparietal.....	Minimally ossified with large fontanelle extending from sphenethmoid to occipital ridge.	Ossification extensive anteriorly with narrow medial separation; fontanelle largest in parietal region.	Ossification extensive anteriorly with narrow medial separation; fontanelle largest in parietal region.	Ossification moderately extensive anteriorly; medial separation of about uniform width throughout length of fontanelle.
Nasals.....	Moderately long and slender; arcuate in dorsal view.	Moderate in size; slightly wider anteriorly than posteriorly in dorsal view.	Moderate in size; slightly wider anteriorly than posteriorly in dorsal view.	Long and broad; arcuate in dorsal view.
Sphenethmoid.....	Extremely short in dorsal view.	Moderately short in dorsal view.	Moderately short in dorsal view.	Moderately short in dorsal view; ossified anteriorly between nasals.
Columella.....	Distal end greatly expanded.	Distal end slightly expanded or not.	Distal end not expanded.	Distal end not expanded.

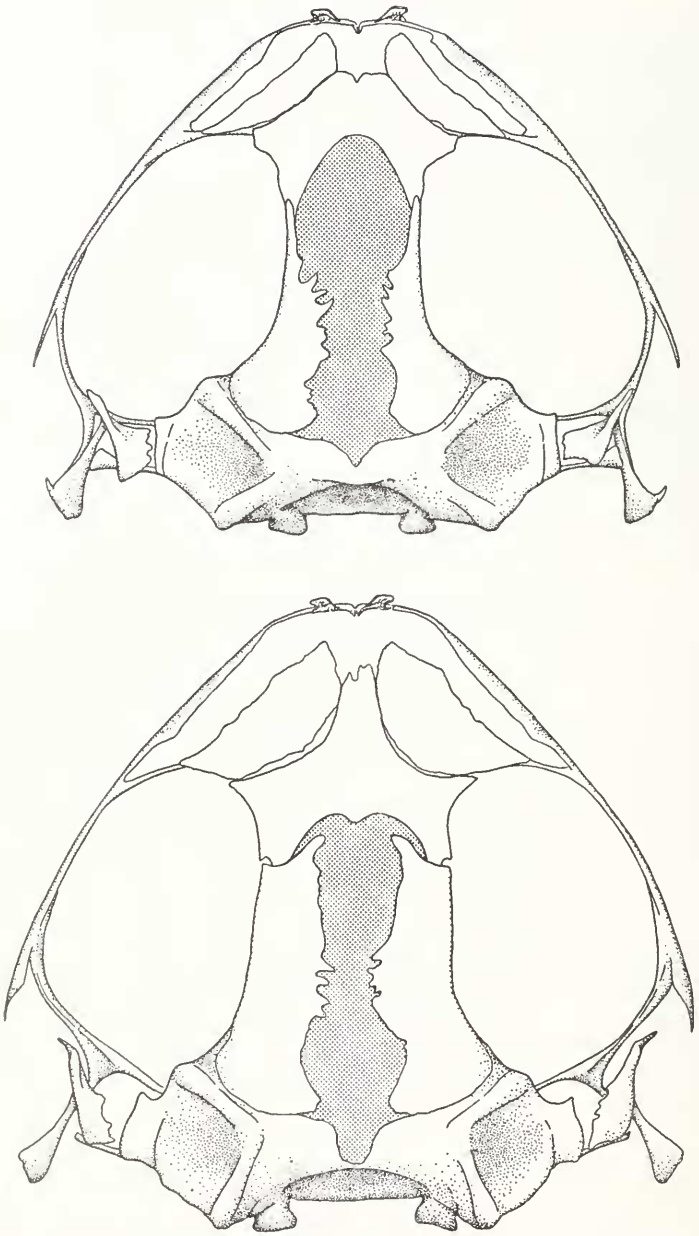


FIG. 5. Dorsal views of the skulls of (a) *Hyla m. microcephala* (KU 68293) and (b) *H. sartori* (UMMZ S-2677). Both × 12.

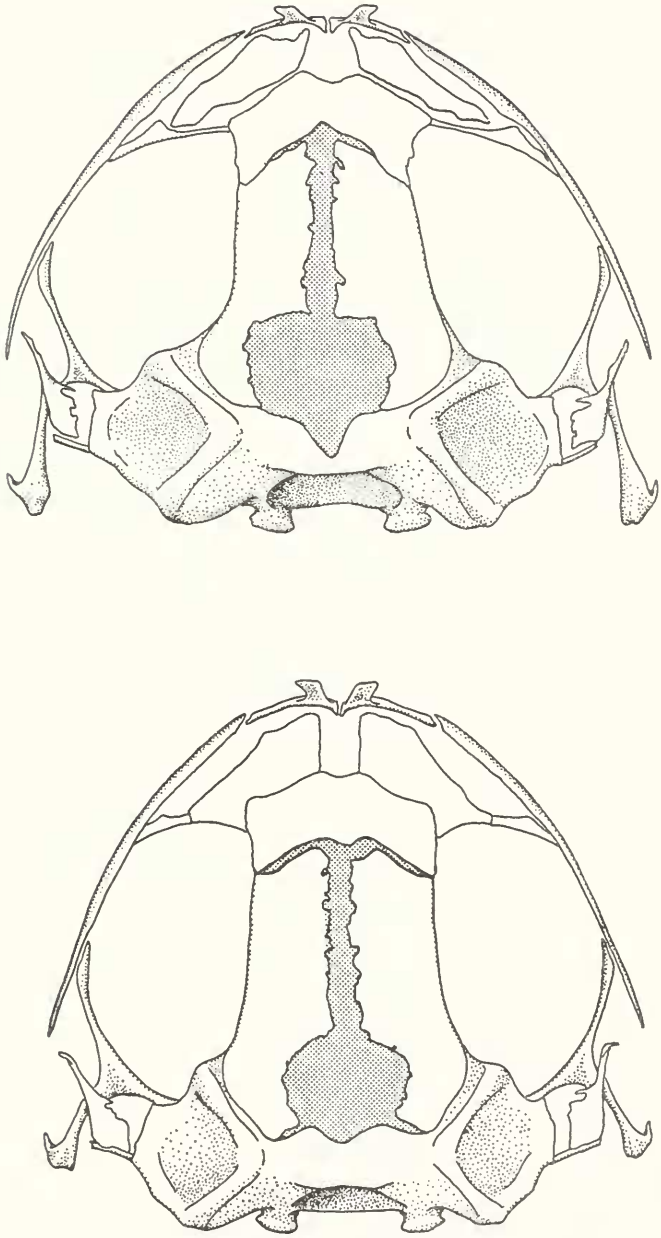


FIG. 6. Dorsal views of skulls of (a) *Hyla phlebodes* (KU 68303) and (b) *H. robertmertensi* (KU 59917). Both × 12.

the species seem to be consistent. The most notable differences are: 1) amount of ossification of the frontoparietals and consequent shape and size of the frontoparietal fontanelle, 2) shape of the nasals, 3) shape and extent of the sphenethmoid, and 4) shape of the columella (Table 4, Figs. 5-6). On the basis of these characters, *Hyla microcephala* can be set apart from the other species and characterized as having a poorly ossified frontoparietal and correspondingly large frontoparietal fontanells; long, slender, arcuate nasals; extremely short sphenethmoid; and expanded distal end of the columella. The other species in the group (*phlebodes, robertmertensi,* and *sartori*) have more ossification of the frontoparietals, broader nasals, only a moderately short sphenethmoid, and an unexpanded distal end of the columella. Among these three species, the skulls of *phlebodes* and *robertmertensi* are most nearly alike, whereas the skull of *sartori* differs by having a differently shaped frontoparietal fontanelle, broader nasals, and an ossified anterior extension of the sphenethmoid between the nasals (compare Fig. 5b with Fig. 6 a-b).

Although all skulls examined belong to breeding adults, the extent of the ossification of the frontoparietals and the resulting shape of the frontoparietal fontanelle might be correlated with the age of the frog. Nevertheless, in the 24 skulls of *Hyla microcephala* examined, the frontoparietals are less extensively ossified than in the skulls of the other species. The trivial differences among the other three species certainly are suggestive of close relationship, but on the basis of present knowledge of the evolutionary trends in hylid cranial osteology, the differences offer little evidence for determining phylogenetic lineage.

ANALYSIS OF MATING CALLS

Calls of all five taxa were compared in several characteristics, of which three are deemed most significant systematically. These are 1) the pattern and duration of the notes of a call-group, 2) the fundamental frequency, and 3) the dominant frequency. Air temperatures were noted at the time the calls were recorded, but no valid correlation could be determined between this factor and any of the parameters of the calls; consequently recordings made at all temperatures (21-29° C.) were grouped together.

Pattern and duration of notes.—In all five taxa the basic pattern consists of a call-group made up of one primary note followed by a series of shorter secondary notes. In some species the secondary

notes differ from the primary in other characteristics. Both subspecies of *Hyla microcephala* have a long, unpaired primary note followed by 0 to 18 (usually about 4) somewhat shorter paired secondary notes. In calls of *Hyla m. microcephala* the mean duration of the primary is 0.131 (0.10-0.16) second and that of the secondaries is 0.101 (0.05-0.14) second, whereas in *H. m. underwoodi* the mean duration of the primary is 0.018 (0.05-0.15) second and that of the secondaries is 0.086 (0.06-0.11) second.

Hyla robertmertensi has a reverse of this pattern in that the primary note is paired and the secondaries are unpaired. In the sample studied a call-group contains 0-28 secondary notes (generally about 3). The mean duration of the primary is 0.091 (0.07-0.11) second and that of the secondaries is 0.040 (0.025-0.06) second.

Hyla phlebodes and *sartori* have call-groups composed of a rather short, unpaired primary and several short, unpaired secondaries (0-28 in *phlebodes,* 0-23 in *sartori*). The mean duration of the primary of *phlebodes* is 0.105 (0.07-0.16) second and that of the secondaries is 0.067 (0.035-0.12) second. The mean duration of the primary of *sartori* is 0.080 (0.07-0.09) second and that of the secondaries is 0.053 (0.035-0.07) second.

The two subspecies of *H. microcephala* are identical in call pattern and agree closely in duration of notes, although those of the nominate subspecies tend to be slightly longer. *Hyla robertmertensi* is distinctive in call pattern in that it is the only species having a paired primary; the duration of the primary is completely overlapped by that in the other species, but the secondaries tend to be the shortest in the group. The call patterns of *H. phlebodes* and *H. sartori* are identical and the range of duration of notes of *phlebodes* completely overlaps that of *sartori,* although both the primary and secondary notes of the latter tend to be somewhat shorter (Table 5, Pl. 16).

Fundamental frequency.—This parameter was analyzed for the primary notes. It was measured for the secondaries as well and was found to differ in magnitude in the same way as the primary note. In a few examples of both subspecies of *H. microcephala* a high prrimary note, in which the fundamental frequency is exceptionally high, is sometimes emitted (Fouquette, 1960b). None of these notes was used in this analysis; only the fundamental frequencies of normal primary notes are compared (Table 5, Fig. 7).

The two subspecies of *H. microcephala* agree closely in fundamental frequency. There is considerable overlap, but the difference between the means is significant at the 0.001 level of probability ($t = 4.2406$). The call of *H. robertmertensi* does not overlap that

TABLE 5.—Comparison of Normal Mating Calls in the Hyla microcephala Group. (Observed Range Given in Parentheses Below Mean; Unless Otherwise Noted Data Are for Primary Notes.)

SPECIES	N	Dominant frequency (cps)	Fundamental frequency (cps)	Duration of notes (seconds)		Repetition rate of secondaries (notes/minute)
				Primary	Secondary	
H. m. microcephala	44	5637 (5150–5962)	205 (184–244)	0.13 (0.11–0.16)	0.10 (0.05–0.14)	268 (192–353)
H. m. underwoodi	47	5772 (5177–6200)	220 (192–275)	0.11 (0.05–0.15)	0.09 (0.06–0.11)	283 (197–384)
H. robertmertensi	25	5388 (5150–5785)	162 (140–178)	0.09 (0.07–0.11)	0.04 (0.03–0.06)	418 (368–570)
H. phlebodes	34	3578 (3220–4067)	148 (125–158)	0.11 (0.07–0.16)	0.07 (0.04–0.12)	284 (210–350)
H. sartori	10	3217 (2950–3600)	126 (116–135)	0.08 (0.07–0.09)	0.05 (0.04–0.07)	434 (396–477)

of *H. sartori* or either subspecies of *H. microcephala* in this parameter; but it does overlap that of *H. phlebodes,* although again the difference between the means is significant at the 0.001 level ($t = 9.360$). *Hyla phlebodes* and *sartori* have the lowest fundamental frequencies, and there is some overlap, but here too the difference between the means is significant at the 0.001 level ($t = 4.923$).

Dominant frequency.—A dominant band of of frequencies cuts across the harmonics of the fundamental, obscuring the harmonic pattern and generally shifting upward in frequency. The midpoint of this band is measured at the terminal border as the dominant frequency. As with the fundamental frequency, only the normal primary notes were utilized in the comparisons (Table 5, Fig 8).

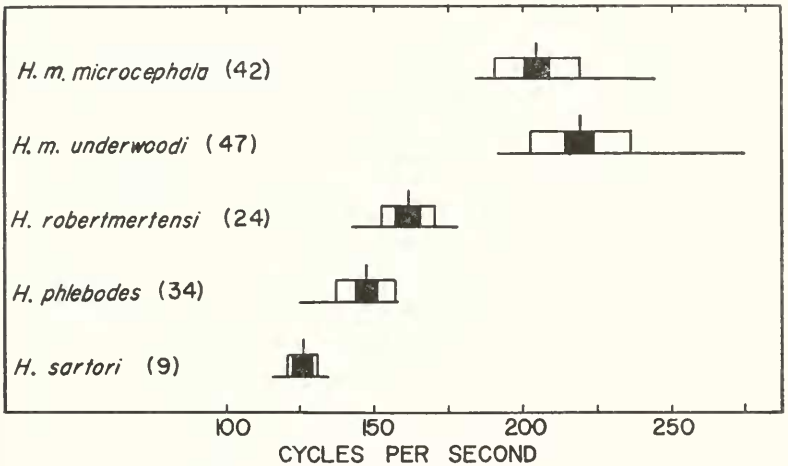


FIG. 7. Variation in the fundamental frequency of the normal primary notes in the *Hyla microcephala* group. The horizontal lines = range of variation, vertical lines = mean, solid bars = twice the standard error of the mean, and open bars = one standard deviation. The number of specimens in each sample is indicated in parentheses after the name of the taxon.

The two subspecies of *H. microcephala* agree more closely in this parameter than in fundamental frequency. The overlap is great, but the difference between the means is significant at the 0.001 level ($t = 3.658$). The calls of both subspecies completely overlap that of *robertmertensi* in this parameter, but the difference between the means is significant at the 0.001 level. The calls of *H. phlebodes* and *H. sartori* overlap considerably in this characteristic, although the difference between the means is significant at the 0.001 level ($t = 7.504$) (Fig. 9). The call of neither species overlaps those of *H. microcephala* and *robertmertensi.*

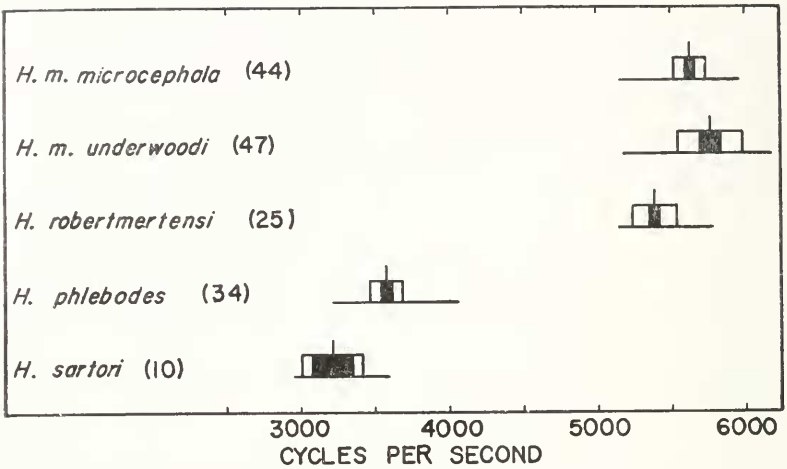


FIG. 8. Variation in the mid-point of the dominant frequency band of the normal primary notes in the *Hyla microcephala* group. The horizontal lines = range of variation, vertical lines = mean, solid bars = twice the standard error of the mean, and open bars = one standard deviation. The number of specimens in each sample is indicated in parentheses after the name of the taxon.

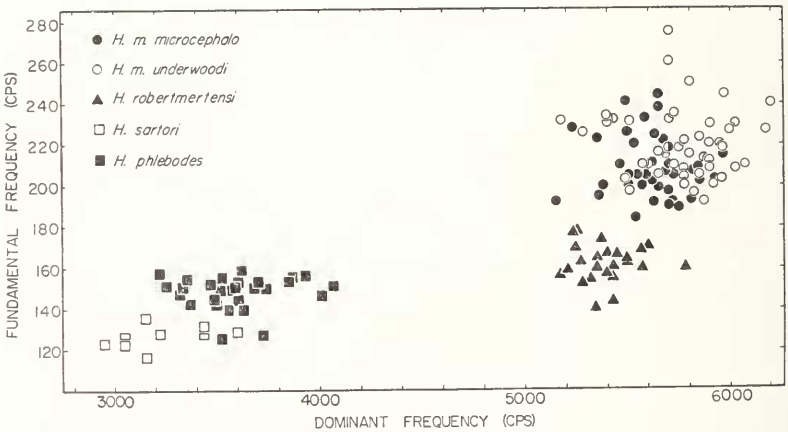


FIG. 9. Scatter diagram relating the dominant and fundamental frequencies of the normal primary notes in the *Hyla microcephala* group. Each symbol represents a different individual.

Repetition rate.—The repetition rate of the secondary notes, in calls consisting of more than one secondary, was measured for each form. A considerable amount of variation in this parameter was found in all of the taxa (Table 5). This variation probably is due in part to the effect of temperature differences. Repetition rate is

the only parameter analyzed for which there is a correlation with the air-temperature, but even here the correlation is weak, probably due to the microenvironmental effects of humidity, air-movement, and other factors in addition to the ambient air temperature that influences the body temperature of the frogs. These rates are nearly alike in both subspecies of *H. microcephala* and in *phlebodes*. The repetition rates in *H. robertmertensi* and *H. sartori* are considerably faster than in the other three taxa. *Hyla sartori* has the fastest repetition rate of the group.

In all characteristics of the mating calls the two subspecies of *H. microcephala* agree closely, as might be expected, although the differences are statistically significant. *Hyla robertmertensi* is distinctive in call pattern and seems to be closer to *microcephala* in dominant frequency but closer to *H. phlebodes* in fundamental frequency. Thus, it is somewhat intermediate between *microcephala* and *phlebodes*. The identical pattern and similarity in fundamental and dominant frequencies of the calls of *H. phlebodes* and *H. sartori* possibly indicate close relationship.

Geographic variation in call.—Hyla m. microcephala has higher fundamental and dominant frequencies in Costa Rica than in Panamá. In Costa Rican *H. m. underwoodi* the fundamental and dominant frequencies are lower than in other parts of the range. Frogs of this subspecies recorded in Nicaragua and Honduras have slightly lower dominant frequencies and higher fundamental frequencies than those recorded in Guatemala or Oaxaca. The duration of both primary and secondary notes decreases to the south; samples from Nicaragua and Costa Rica have the shortest notes. Comparison of duration of notes in the two subspecies shows that the Panamanian *H. m. microcephala* have slightly longer notes than do any *H. m. underwoodi;* the more northern populations of *H. m. underwoodi* from México most closely approach *H. m. microcephala* in this characteristic.

The calls of *H. robertmertensi* in Oaxaca have higher dominant and fundamental frequencies and longer secondary notes than do those in Chiapas.

The calls of *H. phlebodes* recorded at Puerto Viejo, Costa Rica, have slightly lower dominant frequencies than do those recorded at Turrialba, Costa Rica, and in Panamá, whereas those recorded at Turrialba have lower fundamental frequencies than in other samples. The duration of notes is slightly shorter in both Costa Rican samples than in those recorded in Panamá.

LIFE HISTORY

The frogs of the *Hyla microcephala* group breed in shallow grassy ponds. In some places they breed in permanent ponds, but usually congregate around temporary pools, such as depressions in forests, flooded fields, and roadside ditches. At the height of their breeding season, usually in the early part of the rainy season, the congregations are made up of large numbers of individuals. In April, 1961, and in June, 1966, the senior author noted nearly continuous choruses of *H. m. microcephala* in roadside ditches along the 75 kilometers of road between Villa Neily and Palmar Sur, Puntarenas Province, Cost Rica; on June 20, 1966, at Puerto Viejo, Heredia Province, Costa Rica, he estimated approximately 900 *Hyla phlebodes* in one pond, and two nights later noticed that the number of individuals ad increased substantially. Other observations by the first author on size of breeding congregations include nearly continuous choruses of *H. m. underwoodi* between Villahermosa and Teapa, Tabasco, in July of 1958, an estimated 400 *Hyla robertmertensi* in a road side ditch 7.2 kilometers west-northwest of Zanatepec, Oaxaca, on July 13, 1956, and approximately 150 *Hyla sartori* around a rocky pool in a riverbed, 11.8 kilometers west-northwest of Tierra Colorada, Guerrero, on June 28, 1958.

The length of the breeding season seemingly is more dependent on climatic conditions in various parts of Middle America than on behavioral differences in the various species. Thus, Fouquette (1960b) found in the Canal Zone that *H. m. microcephala* formed breeding choruses from May through January, the entire rainy season in that area. In the wetter coastal region of Puntarenas Province, Costa Rica, the species breeds as early as mid-March, whereas in the drier region encompassing Guanacaste Province, Costa Rica, and southwestern Nicaragua breeding activity is initiated by the first heavy rains of the season, usually in June.

Hyla phlebodes inhabits regions having rainfall throughout the year. Although large breeding congregations are most common in the early parts of the rainy season, males probably call throughout the year. At Puerto Viejo in Costa Rica the senior author has heard *Hyla phlebodes* in February, April, June, July, and August. Charles W. Myers noted calling males of this species in the area around Almirante, Bocas del Toro Province, Panamá, in September, October, and February. An exception to the correlation between rainfall and breeding activity was noted by the junior author in *Hyla phlebodes* in the Canal Zone, where he noticed a decrease in activity of that species in October and November, when the rains are heaviest and

most frequent. Furthermore, independent observations made by both of us indicate that *H. phlebodes* does not reach peaks of activity during or immediately after heavy rains, but instead builds up to peaks of activity two or three days after a heavy rain. This is in contrast to the other species, all of which characteristically inhabit drier environments than does *H. phlebodes*. Peaks of breeding activity in the other species occur immediately after, or even during, heavy rains.

The calling location of the males generally is on vegetation above, or at the edge of, the water. *Hyla microcephala* and *H. phlebodes* call almost exclusively from grasses and sedges; *phlebodes* usually calls from taller and more dense grasses than does *microcephala*. Except for some minor differences in calling location observed by the junior author (Fouquette, 1960b) in the Canal Zone, the differences in density and height of grasses utilized for calling-locations probably is dependent primarily on the nature of the available vegetation. Although bushes and broad-leafed herbs are usually present at the breeding sites, males of these species seldom utilize them for calling locations. Both *H. robertmertensi* and *H. sartori* have been observed calling from grasses, herbs, bushes, and low trees. Calling males of *robertmertensi* have been found two meters above the ground in small trees.

Daytime retreats in the breeding season sometimes are no more than shaded clumbs of vegetation adjacent to a pond or in clumps of grass in a pond. Individuals of *H. m. underwoodi* were found by day under the outer sheaths of banana plants next to a water-filled ditch. Dry season refuges are unknown.

Amplexus is axillary in all four species. Egg deposition has been observed in *H. m. microcephala, m. underwoodi,* and *phlebodes*. In all three the eggs are deposited in small masses that float near the surface of the water and usually are at least partly attached to emergent vegetation. Each clutch does not represent the entire egg complement of the female.

Tadpoles are definitely known of only *H. m. microcephala* and *phlebodes;* these have been described in the preceding accounts of the species. The tadpoles of these two species can be distinguished readily (Pl. 15). The tadpole of *H. microcephala* has a uniformly white venter and nearly transparent tail, whereas in *H. phlebodes* the venter is flecked anteriorly and the tail is mottled. In life, *H. microcephala* is easily recognized by the orange posterior half of the tail, whereas the tail in *H. phlebodes* is mottled tan and grayish brown.

PHYLOGENETIC RELATIONSHIPS

The evidence already presented on osteology, external structure, coloration, mating call, and life history emphatically show that the four species under consideration are a closely related assemblage. Now the question arises: To what other groups in the genus is the *Hyla microcephala* group related? Furthermore, it is pertinent to this discussion to attempt a reconstruction of the phylogeny of the group as a whole and of the individual species in the *Hyla microcephala* group. With regard to the relationships of the group we must take into account certain species in South America. Our endeavors there are hampered by the absence of data on the mating calls and life histories of most of the relevant species.

As mentioned in the acount of *Hyla m. microcephala,* the species *microcephala* possibly is subspecifically related to *Hyla misera,* a frog widespread in the Amazon Basin. *Hyla misera* resembles *microcephala* in coloration, external structure, and cranial characters. The frontoparietals are equally poorly ossified, and the frontoparietal fontanelle is extensive. Our principal reason for not considering the two taxa conspecific at this time is our lack of knowledge concerning the color of living *H. misera,* the structure of the tadpoles, and the characteristics of the mating call. Even with the absence of such data that we think essential to establish the nomenclature status of the taxa, we are confident that the two are sufficiently closely related that any discussion of the phylogenetic relationships of one species certainly must involve consideration of the other.

Hyla misera possibly is allied to other small yellowish tan South American *Hyla* that lack dark pigmentation on the thighs. Probable relatives are *Hyla elongata, minuta* (with *goughi, pallens, suturata, velata,* and possibly others as synonyms), *nana,* and *werneri.* The consideration of the interspecific relationships of these taxa is beyond the scope of this paper, but we can say that each of these species has a pale yellowish tan dorsum, relatively broad dorsolateral brown stripe, and narrow longitudinal brown lines or irregular marks on the dorsum. Furthermore, examination of the skulls of *elongata, nana,* and *werneri* reveals that they are like *misera* and *microcephala* in the nature of the frontoparietal fontanelle and in having a greatly reduced quadratojugal. Thus, on the basis of cranial and external characters the *Hyla microcephala* group can be associated with *Hyla misera* and its apparent allies in South America. This association can be only tentative until the mating calls, tadpoles, and chromosome numbers of the South American species are known.

Among the Middle American hylids, only the *Hyla microcephala* group and *H. ebraccata* have a haploid number of 15 chromosomes (Duellman and Cole, 1965). All other New World *Hyla,* for which the number is known, have a haploid number of 12; the only other *Hyla* having 15 is a Papuan *Hyla angiana* (Duellman, 1967).

Hyla ebraccata occurs in the humid tropical lowlands of Middle America and the Pacific lowlands of northwestern South America. It is the northernmost, and only Central American, representative of the *Hyla leucophyllata* group, which is diverse (about 10 species currently recognized) and widespread in tropical South America east of the Andes. This group is characterized by having broad, flat skulls with larger nasals and more ossification of the frontoparietals than in the *Hyla microcephala* group. The quadratojugal is present as a small anteriorly projecting spur that does not connect with the maxillary. Externally, the *Hyla leucophyllata* group is characterized by having a well-developed axillary membrane, uniformly yellow thighs, and a dorsal color pattern in many species consisting of a dark lateral band, a pale dorsolateral band or dorsal ground color, and a large middorsal dark mark. In some species, the dorsal pattern consists of small dark markings or is nearly uniformly pale. At least in the Central American *Hyla ebraccata,* the mating call consists of a single primary note followed by a series of shorter secondary notes, the tadpoles have xiphicercal tails and lack teeth, and the haploid number of chromosomes is 15. On the strength of these observations it seems imperative to consider the *Hyla leucophyllata* group as a close ally to the *Hyla microcephala* group. Successful artificial hybridization supports the close relationship of *H. m. microcephala* and *phlebodes;* partial success of artificial hybridization of these two with *ebraccata* (Fouquette, 1960b) provides further evidence for close relationship between the *Hyla leucophyllata* and *Hyla microcephala* groups.

In México and northern Central America two small species, *Hyla picta* and *Hyla smithi,* comprise the *Hyla picta* group. These frogs resemble members of the *Hyla microcephala* group by having a yellowish tan dorsum with a dorsolateral white stripe and uniformly yellow thighs. Furthermore the mating call is not unlike those of the species in the *Hyla microcephala* group. Despite these similarities, the *Hyla picta* group differs from the *Hyla microcephala* group by having a well-developed quadratojugal that connects to the maxillary, tadpoles with teeth present and caudal fins completely enclosing the caudal musculature, and a haploid number of 12 chromosomes. In all of these characteristics the frogs of the